

Assessing the risk of invasion by a vineyard moth pest guild

Hector Zumbado-Ulate¹, Tyler E. Schartel²,
Gregory S. Simmons³, Matthew P. Daugherty¹

1 Department of Entomology, University of California, Riverside, CA 92521, USA **2** Prairie Research Institute, Illinois Natural History Survey, University of Illinois at Urbana/Champaign, 1816 South Oak Street, Champaign, IL 61820, USA **3** United States Department of Agriculture, Animal Plant Health Inspection Service, Plant Protection and Quarantine, Science and Technology, Salinas, CA 93905, USA

Corresponding author: Hector Zumbado-Ulate (zumbadohector@gmail.com)

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Abstract

Biological invasions are most effectively managed when identified in their early stages, which often hinges on robust surveillance programs. The recent invasion of the European grapevine moth (*Lobesia botrana*) in California suggests that viticultural areas in the western United States may face severe economic consequences from this and other Tortricid and Pyralid moth species if they were to establish. To gain insights into the risk these grapevine pests pose, we used occurrence records for *L. botrana* and four other moths native to Europe or the eastern United States and selected environmental variables to predict the extent of climatically suitable areas and potential pest co-occurrence along the West Coast of the United States. A suite of models was generated using MaxEnt with species-specific tuning of model settings. Overall, the results confirmed high suitability for *L. botrana* to establish across much of the study region, driven largely by high monthly variability in precipitation and low elevation. Two species were predicted to have intermediate suitability to establish over the study region (i.e., grape tortrix moth, *Argyrotaenia ljungiana*; grape berry moth, *Paralobesia viteana*), while two others had low suitability (i.e., European grape berry moth, *Eupoecilia ambiguella*; Christmas berry webworm, *Cryptoblabes gnidiella*). The highest predicted potential for co-occurrence was between *L. botrana* and *P. viteana*, accounting for 19% of the total viticulture area, followed by *L. botrana* and *A. ljungiana* for 11% of the study area. These results may help with the optimization of surveillance efforts by indicating which species or areas should be prioritized for the deployment of invasive pest detection programs with pheromone traps. Indeed, given the apparent potential for co-occurrence of multiple moth pests in certain areas, our results may inform where single or multi-lure traps should be deployed as a more cost-efficient monitoring tool.

Keywords

detection trapping, invasion risk, pest surveillance, species distribution model

Introduction

Invasive species are a significant threat to global biodiversity (Richardson et al. 2000; Gurevitch and Padilla 2004) that can have detrimental effects on other species and economic productivity (Meyerson et al. 2019; Shackleton et al. 2020). Human-mediated mechanisms of pest invasions, which include the introduction of pest species into new environments, naturalization, and further spread disturb many native species through predation, competition for limited resources, transmission of pathogens, and disruption of behavioral processes (Pyšek and Richardson 2010; Hoffmann and Courchamp 2016). For agroecosystems, invasive species may precipitate increased costs and substantial production and revenue losses (Paini et al. 2016; Savary et al. 2019). As a result, government agencies and industry groups devote enormous resources to identifying and eradicating established invasive species. However, invasive species management is most efficiently achieved during the initial stages of an invasion, when invader abundance is low (Simberloff et al. 2013; Bradley et al. 2019). Further research is needed to expedite robust responses to invasive species arrival (Leung et al. 2002).

Biological invasions in the United States cost more than \$100 billion annually and are increasing in frequency (Pimentel et al. 2005; Simberloff et al. 2013; Meyerson et al. 2019; Crystal-Ornelas et al. 2021). According to the United States Animal and Plant Health Inspection Service (APHIS; <https://www.aphis.usda.gov/>), invasive insects have caused significant losses to the US environment and economy, particularly with respect to native forests and a wide range of annual and perennial crops. Such effects may be pronounced in states with large agricultural enterprises, such as California. Between 1990 to 2010, it is estimated that approximately 10 exotic arthropod species were introduced into California each year, 20% of which became significant pests (Dowell et al. 2016). This represents a 62% increase in introductions compared to 1970–1989 despite more rigorous border controls and monitoring programs, reinforcing the need for additional research to anticipate the arrival and ultimate impact of invasive species.

A recent invader of particular importance to California's wine, raisin, and table grape industry is the European grapevine moth (EGVM), *Lobesia botrana* (Lepidoptera: Tortricidae) [Denis & Schiffermüller]; one of several Lepidopteran agricultural pests that have proven capable of rapid geographic range expansion (Suckling et al. 2017). This phytophagous species uses multiple plant species but particularly cultivated grapevines, where its larvae feed on flowers and grape berries, causing direct damage and introducing fungal rots, which can dramatically reduce yields (Delbac and Thiéry 2016). Although the native range of EGVM includes much of Europe, it has successfully invaded other regions, such as western and northern Africa (Ioriatti et al. 2012;

Lucchi and Scaramozzino 2022) and grape-growing regions in the Americas, including Chile, Argentina, and the United States (Varela et al. 2010; Gilligan et al. 2011).

In the United States, EGVM was first detected in California in late 2009 (Gilligan et al. 2011). Following initial detections in select areas of Napa County, more extensive monitoring showed it had spread to several surrounding areas. In 2010, more than 100,000 male moths were caught on nearly 4,000 pheromone traps. EGVM was ultimately recorded in 11 counties in Northern and Central California, up to approximately 300 km from where it was initially detected (Simmons et al. 2021). In response, an eradication program was established that included state-wide monitoring with pheromone traps, insecticide treatments, mating disruption, and a regulatory control program. Subsequently, sharp declines in EGVM captures were seen over the next few years to the point that it was declared eradicated in 2016, following two years without any detections (Schartel et al. 2019; Simmons et al. 2021).

As part of a larger study evaluating the factors that contributed to the successful eradication of EGVM in California, Schartel et al. (2019) used occurrence records from the state-wide monitoring program to develop a suite of habitat suitability models for EGVM in Napa County. The results showed select climatic, landscape, and anthropogenic variables explained observed patterns in EGVM occurrence, but generated uncertainty regarding EGVM suitability in the study region, perhaps due to confounding effects of generating suitability estimates during an eradication program (Schartel et al. 2019). Moreover, occurrence records from the program data were insufficient to evaluate suitability for EGVM in other areas of California, let alone for viticultural areas in neighboring states along the West Coast. Thus, while EGVM is considered a threat should it be reintroduced into the region, questions remain about the magnitude of that risk and the specific locations most likely to be affected.

EGVM is only one of several moth pests of grapevines with the potential to be highly destructive. Other species in the families Tortricidae and Pyralidae have proven to be significant pests in other viticultural regions (Ioriatti et al. 2012; Isaacs et al. 2012), and are considered high risk by the California grape industry (Napa County California 2022) or have been included as priority targets by the national Cooperative Agricultural Pest Survey (2022). These species may threaten vineyards along the West Coast of the United States should they be introduced: grape tortrix moth (GTM); *Argyrotaenia ljungiana* (Lepidoptera: Tortricidae) [Thunberg]), grape berry moth (GBM); *Paralobesia viteana* (Lepidoptera: Tortricidae) [Clemens]), European grape berry moth (EGBM); *Eupoecilia ambiguella* (Lepidoptera: Tortricidae) [Hübner]), and Christmas berry webworm (CBW); *Cryptoblabes gnidiella* (Lepidoptera: Pyralidae) [Millière]). EGBM, GTM and CBW occur naturally in Europe (similar to EGVM) but have invaded portions of Asia, Africa and Oceania (Ostrauskas et al. 2008; Ioriatti et al. 2012). Meanwhile, GBM is native to central and eastern United States, where it shows high fidelity to wild and cultivated grapes, causing significant yield losses (Botero-Garcés and Isaacs 2003; Isaacs et al. 2012). Damage to grapevines varies among species but is generally a function of larval infestation levels that are themselves influenced by characteristics of the grapevine (e.g., cultivar) and climatic conditions that influence moth

phenology and voltinism (Ioriatti et al. 2012). Direct damage from larval feeding can result in minor to extensive reduction in fruit yields, and can facilitate fungal infections or secondary pest infestations (Moschos 2006; Ioriatti et al. 2012; Isaacs et al. 2012).

Monitoring using pheromone-baited traps is commonly employed for pest management, and for early detection of invasive insects (McNeil 1991; Vacas et al. 2011). Maintaining long-term surveillance programs for high-risk pests is costly, but the costs of missing the detection of a newly arrived pest may quickly exceed surveillance costs if the new pest is allowed to spread beyond a point where eradication is feasible (Chase et al. 2018). Hence, there is a need to prioritize the placement of traps in areas that are most conducive to pest establishment so that the limited resources available for pest detection are optimized. Yet, current knowledge gaps regarding the invasive potential of EGVM and these other grape pest moths hamper optimization of those surveillance programs.

We gathered occurrence records from the native and invaded ranges of five high-risk lepidopteran pests of grapevines and selected a number of environmental variables to quantify invasion risk along the West Coast of the United States (Cooperative Agricultural Pest Survey 2022; Napa County California 2022) (Suppl. material 1: fig. S1). The goals of these analyses were to a) estimate the overall invasive potential of each species throughout viticultural areas in the Western United States, b) identify those locations most at risk to the establishment of each species and the environmental conditions that underlie them, and c) identify areas where multiple moth species are likely to co-occur if introduced. Although none of these species currently occur in the region, the threats posed by their introduction, and the potential for multiple species to establish in the same region, warrant further investigation to inform implementation of early detection and surveillance efforts (Cooper et al. 2014; Simmons et al. 2021).

Methods

Study region and focal species

We focused on the invasive potential of five grapevine pests (EGBM, EGVM, GBM, GTM, and CBW) in grape-growing regions along the West Coast of the United States, in portions of California, Oregon, and Washington (5–40°N, 70–118°W; Suppl. material 1: fig. S1). Overall, the study region represents a substantial portion of the high-value grape acreage in the United States and is the only region where one of these moth pests has successfully invaded (Gilligan et al. 2011). Moreover, states along the West Coast include many pathways that could contribute to pest arrival and spread (Dowell et al. 2016). The West Coast covers approximately 835,905 km² and has a wide variety of physiographic characteristics. The climate varies across the study region, but overall, the region receives most precipitation during the winter months (Neiman et al. 2008). Most grape-growing regions have been officially classified into American Viticulture Areas (AVAs), which are established by the Alcohol and Tobacco Tax and Trade Bureau under the US Department of the Treasury. Shapefiles of AVAs were obtained from the

American Viticultural Area Project at the University of California-Davis (<https://github.com/UCDavisLibrary>). We supplemented California AVAs boundaries with California Department of Water Resources (DWR) polygons depicting 2016 wine-grape growing vineyards (<https://gis.water.ca.gov>), which included wine, raisin and table grapes areas. The boundaries of DWR polygons were dissolved and a 10 km radius buffer was added to grape-growing locations to capture newly established vineyards (since 2016) in the immediate vicinity. Then, these supplemental vineyards were joined with the AVAs boundary polygons to create a final GIS-referenced shapefile of viticultural areas in the study region, which encompassed 21.4% (178,922 km²) of the West Coast of the United States. All study analyses were conducted with the R statistical language V 4.2.2 (R Core Team 2022) and ArcGIS Pro 3.0.1 (ESRI Redlands, CA, USA). Country-level shapefiles were obtained from the Database of Global Administrative Areas (<https://gadm.org>).

Occurrence datasets and predictor variables

Risk assessments based on extrapolations of species distribution model (SDM) predictions to regions and periods different from the conditions used to calibrate the model (i.e., model transferability) are effective for pest management and species conservation planning (Heikkinen et al. 2012; Barbet-Massin et al. 2018). It is recommended that species occurrences in both native and non-native ranges be used when developing SDMs to assess invasion risk in newly invaded or at-risk regions (Jiménez-Valverde et al. 2011; Peterson 2011; Jarnevich et al. 2022).

We downloaded occurrence data for all five pest species in their native and other invaded ranges from 1960 to the present date from the Global Biodiversity Information Facility (GBIF; www.gbif.org; Suppl. material 1: figs S2–S6). For EGVM occurrences we also included records from its invasion into Napa County (Schartel et al. 2019). Regarding GBIF records, we only considered those provided by 1) official institutions and biological collections and 2) data citizen science platforms only when the species ID was previously confirmed by specialists. Then, occurrence datasets were cleaned by checking for typos, removing unreferenced records, cross-checking geographic coordinates, and removing coordinates with a geographic inaccuracy > 10000 m. A collection of background points to specific areas was generated by buffering known occurrences in pest native and non-native ranges with a 50 km radius buffer (i.e., calibration areas). The final number of background points differed among species because of the different sizes of the calibration areas and corrections for sampling bias. To reduce the effect of spatial autocorrelation in both occurrence and background datasets, we excluded points that were separated by a distance < 1 km. Final presence-only datasets consisted of 467 occurrence records for EGBM, 459 for EGVM, 54 for GBM, 644 for GTM, and 121 for CBW. Final background datasets consisted of 12331 background points for EGBM, 6741, for EGVM, 3125 for GBM, 14991 for GTM, and 1784 for CBW.

All 19 BIOCLIM variables (Booth et al. 2014) and the global elevation layer were downloaded from WorldClim 2.1 (Fick and Hijmans 2017; <https://www.worldclim.org/>), along with 12 of the 14 environmental raster layers from ENVIREM (Title

and Bemmels 2018; <https://envirem.github.io/>). All raster layers were downloaded at 5 min spatial resolution (Suppl. material 1: table S1). Multicollinearity among predictors at moth occurrence and background locations was assessed by estimating the variance inflation factor (VIF) with the R package ‘usdm’ 1.1–18 (Naimi 2015). Specifically, we excluded from our analysis highly correlated variables using a VIF threshold of 0.7.

Species distribution modeling

Here, we provide an overview of our climatic suitability modeling methodology following the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol for species distribution models (Zurell et al. 2020). Specific methodological details for all ODMAP sections are presented as supplementary material (Suppl. material 1: table S2). We used the MaxEnt algorithm (Phillips et al. 2006) with species-specific tuning of model settings implemented through the R package ‘ENMeval’ 2.03 (Kass et al. 2021) to generate continuous predictions of climatic suitability across the native and invaded range (e.g., Zeng et al. 2016; Zumbado-Ulate et al. 2022). The following settings were used to parametrize and generate 16 candidate models for each species: algorithm = maxent.jar; partition method = block; regularization of multiplier values = 1–4 with increments of 1; feature classes = L, H, Q, LQH; where L = Linear, H = Hinge, Q = Quadratic, Clamping = True.

Model selection was conducted using the highest average of the area under the curve of the receiver-operating characteristic (‘AUC mean’), the standardized true skill statistic (sTSS), and the average of the 10-percentile training omission rate (‘10.or.pt mean’). For selected models, we estimated the percent contribution of each selected abiotic predictor and generated response curves by comparing the probability of each pest species’ presence relative to each abiotic predictor (Elith et al. 2006; Syfert et al. 2013). The Boyce index (Boyce et al. 2002), and the slope of the regression of the response variable on the logit of predicted probabilities according to Miller’s calibration statistics (Miller et al. 1991) were estimated to evaluate how much model predictions differed from the random distribution of the observed presences across the prediction gradients and extrapolation of our predictions outside the training data.

Species co-occurrence

To identify areas that may be susceptible to the establishment of multiple moth species, we used two alternative thresholds to generate binary predictions (raster absence-presence maps) of the potential range of each species across the study region. Binary predictions were transformed into polygons to quantify the extent of climatically suitable areas (ESH; Brooks et al. 2019) of each species in square kilometers (km²). Specifically, we used the 10-percentile lowest omission rate logistic threshold (10.or.pt; Radosavljevic and Anderson 2014), which excludes those occurrence points with suitability in the lowest 10 percentile, and the maximum training sensitivity plus specificity logistic threshold (maxSS), which performs an overall true occurrence prediction (Liu et al. 2005). This

approach allowed us to quantify ESH across the study region under two scenarios with different degrees of conservativeness: 1) removing only the 10 percent of the localities having the lowest predicted values of climatic suitability, or 2) maximizing the true positive prediction, resulting in a more restricted definition of climatically suitable areas.

To identify areas of co-occurrence, binary predictions were combined into a single raster. Because the binary predictions only had values of zero and one, the resulting cumulative raster displayed values between zero (no pest species predicted to occur in a pixel) and five. Then, this cumulative raster was transformed into a polygon to estimate the potential co-occurrence of multiple species, from two to five species. To calculate ESH we transformed the projected coordinate system of binary predictions and AVAs from WGS84 to NAD 1983 Albers contiguous USA (ESRI 102003).

Finally, a principal component analysis (PCA) was generated to visualize the environmental space where multiple pest species are predicted to overlap. For this, we selected the ten predictors with highest contributions to the SDMs (Table 1) and simulated 1000 pseudo-occurrences for each study species across the environmental space by generating 1000 random points throughout their climatically suitable areas based on the binary predictions built with the 10.or.pt threshold. All pseudo-occurrences were spatially filtered using a distance of 10 km. Remaining pseudo-occurrences were transformed into cell centroids in grids of 10 km² resolution. This method allowed us to generate a weighted sample size for each pest species according to their ESH and full environmental space.

Results

One preferred model was identified for each species (Suppl. material 1: table S3) from the total set of candidate models (5 species, 80 total models). Selected models varied in feature classes (L, Q, and LHQ), and four of them scored the highest AUC with the regularization multiplier at 1. Overall, both independent and dependent threshold evaluation metrics (Suppl. material 1: table S3) showed that the most robust model for each species exhibited a good fit and performed better than random models: AUC mean values between 0.71 and 0.89, sTSS values between 0.66 and 0.82, and low omission rates (10.or.pt mean values between 0.01 and 0.1). Similarly, the Boyce Index values (between 0.90 and 0.98), and the slope of Miller Calibration statistics (between 0.6 and 1) showed that model predictions were consistent with the distribution of presences in the evaluation dataset and transferred efficiently into a new geographic area.

Sixteen abiotic predictors were retained among the five models selected (Table 1). Elevation was the only predictor featured in all five species models, but mean diurnal range, precipitation seasonality, precipitation of the warmest quarter, minimum temperature of the warmest month, mean monthly potential evapotranspiration of driest quarter, and monthly variability in potential evapotranspiration appeared in four of the selected models. In general, the percent contribution of each selected abiotic predictor matched the percent of permutation importance of each selected abiotic predictor, but with some inconsistencies that may be attributable to modest multicollinearity (Table 1).

Table 1. Percent contribution (% C) and permutation importance (% P) of selected abiotic predictors in species-specific climatic suitability models (EGBM = European grape berry moth, *Eupoecilia ambiguella*; EGVM = European grapevine moth, *Lobesia botrana*; GBM = Grape berry moth, *Paralobesia viteana*; GTM = Grape tortrix moth, *Argyrotaenia ljugiana*; CBW = Christmas berry webworm, *Cryptoblabes gnidiella*). The two predictors with the highest contributions are in bold.

Predictor	EGBM	EGVM	GBM	GTM	CBW
	% C (% P)	% C (% P)	% C (% P)	% C (% P)	% C (% P)
BIO2; Mean diurnal range (°C)	2.7 (0.5)	–	10.5 (25.6)	32.2 (47)	69.5 (20.1)
BIO3; Isothermality (°C)	7.7 (6.8)	6.1 (5.3)	–	35.5 (35.6)	–
BIO7; Temperature annual range (°C)	–	11.4 (13.9)	–	–	–
BIO8; Mean temperature of wettest quarter (°C)	6 (7.8)	3.9 (5.3)	–	0 (0)	–
BIO13; Precipitation of wettest month (mm)	7.1 (14.7)	6.1 (7.2)	–	–	–
BIO14; Precipitation of driest month (mm)	–	–	0 (0)	–	0.7 (7.4)
BIO15; Precipitation seasonality (mm)	2.2 (5.9)	57.6 (42.1)	–	13.5 (2.4)	0.5 (3.7)
BIO18; Precipitation of warmest quarter (mm)	–	0 (0)	27.1 (41.2)	0.2 (0.4)	0 (0.2)
BIO19; Precipitation of coldest quarter (mm)	3.8 (0)	–	–	–	1.2 (0.1)
Elevation (m)	57.6 (57.6)	12.6 (10)	0 (0)	14.4 (1.6)	7.9 (6.1)
EPQ; Emberger’s pluviothermic quotient	–	–	–	0.3 (2.1)	–
gDD5; growingDegDays5 (°C) ¹	4.4 (5.1)	–	–	–	–
mTW; Minimum temperature of warmest month (°C)	–	0.3 (1.3)	56.5 (23)	3.8 (10.5)	12 (0)
PETDQ; PET of driest quarter (mm) ²	–	1.4 (14.1)	3.7 (2.7)	0.1 (0.4)	3.4 (42.1)
PETS; PET seasonality (mm) ²	8.5 (1.6)	0.6 (0.9)	2.2 (7.4)	–	4 (18.2)
PETWQ; PET of wettest quarter (mm) ²	–	–	–	–	0.9 (2.1)

¹sum of mean monthly temperature for months with mean temperature greater than 5 °C multiplied by the number of days.
²potential evapotranspiration.

Of the five focal species evaluated, the area estimated to be moderate to highly climatically suitable for establishment was highest for EGVM, especially along the coastline, in western and central areas of Washington and Oregon, and central regions of California (Fig. 1A, B). The two abiotic predictors with the strongest contribution to EGVM model predictions (Table 1) were seasonal precipitation (58%) and elevation (13%). The highest predicted suitability (0.9) occurred in areas with the high monthly variability in precipitation, and climatic suitability decreased rapidly as elevation increased from a maximum of 0.4 near sea level (Suppl. material 1: fig. S7). The ESH varied between 36 and 65% of the total viticultural area in the study region, depending on which threshold was considered (Table 2).

Climatic suitability was relatively moderate throughout the study region for two pest species. For GBM, the most climatically suitable regions occurred in small patches across viticulture areas in Washington and Oregon, and very small portions along the coast of California (Fig. 2A, B). The minimum temperature during the warmest month (57%) and precipitation during the warmest quarter (27%) had the highest contributions to GBM model predictions (Table 1). Estimated climatic suitability increased gradually as temperature increased, reaching a maximum of 0.8 at approximately 25 °C (Suppl. material 1: fig. S8a). Conversely, estimated climatic suitability decreased rapidly for locations with higher precipitation during the warmest quarter, from a maximum of 0.8 between 0- and 200-mm precipitation to 0.3 at approximately 500 mm (Suppl. material 1: fig. S8b). The ESH predicted for GBM represented between 0%

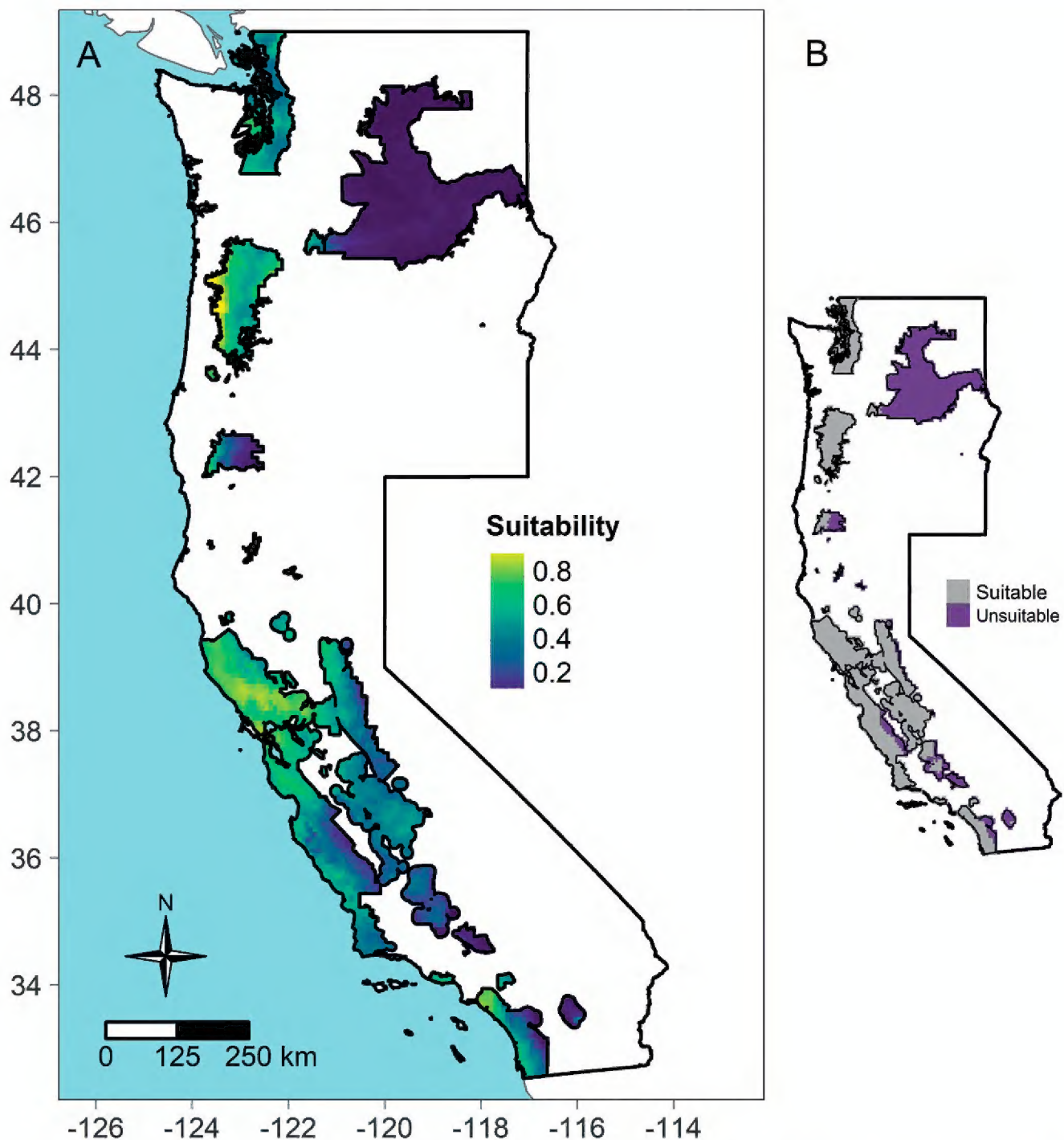


Figure 1. Climatic suitability map for the European grapevine moth (EGVM), *Lobesia botrana*, in viticultural regions along the West Coast of the United States **A** continuous climatic suitability estimates **B** binary predictions of climatically suitable areas based on the 10-percentile lowest omission rate threshold.

and 21% of the total viticulture area (Table 2). For GTM, only the viticulture areas in far northern Washington and small portions of central and southern California were climatically suitable for establishment (Fig. 2C, D). The two abiotic predictors with the highest contribution to the model predictions (Table 1) were isothermality (36%) and mean diurnal range (32%). Estimated climatic suitability across the native and invaded range of the GTM increased as the ratio of diurnal variation to annual variation in temperatures increased, reaching maximum suitability of 0.8 near 50 °C, and decreased for locations where the mean differences between maximum and minimum temperatures were the greatest (Suppl. material 1: fig. S9). The ESH of the GTM represented between 0.1 and 13% of the viticulture areas (Table 2).

Finally, the vast majority of the study region was projected to have relatively low climatic suitability for two focal species. For EGBM, the most climatically suitable

Table 2. Extent of climatically suitable areas (ESH) and corresponding percent of the total area of viticulture regions (% VR) for five moth species (EGBM = European grape berry moth, *Eupoecilia ambiguella*; EGVM = European grapevine moth, *Lobesia botrana*; GBM = grape berry moth, *Paralobesia viteana*; GTM = grape tortrix moth, *Argyrotaenia ljugiana*; CBW = Christmas berry webworm, *Cryptoblabes gni-diella*) using two binary thresholds for suitability: 10-percentile lowest omission rate threshold (10.or.pt) and the maximum training sensitivity plus specificity threshold (maxSS).

Species	Threshold			
	10.or.pt		maxSS	
	ESH (km ²)	% VR	ESH (km ²)	% VR
EGBM	21640	12.1	1134.1	0.6
EGVM	115605	64.6	64894.6	36.3
GBM	36940	20.6	64.8	0.0
GTM	22776	12.7	109.6	0.1
CBW	1074	0.6	123.0	0.1
Number of species ¹	ESH (km ²)	% VR	ESH (km ²)	% VR
0	37917.8	21.2	113329.8	63.3
1	95758.2	53.5	65396.1	36.6
2	34154.6	19.1	115.5	0.1
3	9586.5	5.4	79.6	0.0
4	1402.6	0.8	0.0	0.0
5	101.3	0.1	0.0	0.0

¹number of the five moth species predicted to co-occur in an area.

regions for establishment occurred in central Washington and far northern Oregon (Fig. 2E, F). The two abiotic predictors with the highest contribution to EGBM model predictions were elevation (58%) and monthly variability in potential evapotranspiration (9%; Table 1). Climatic suitability was predicted to be highest (0.8) near sea level and decreased at higher elevations as well as increased over a gradient of increasing precipitation (Suppl. material 1: fig. S10). The ESH represented between approximately 1 and 12% of all viticulture area (Table 2). For CBW, most of the study region was predicted to be climatically unsuitable (Fig. 2G, H). The mean diurnal range and the minimum temperature of the warmest month had the highest contributions to model predictions (Table 1). Estimated climatic suitability gradually decreased as the mean difference between maximum and minimum temperatures increased. Estimated climatic suitability also increased at higher temperatures (Suppl. material 1: fig. S11). The predicted ESH ranged between just 0.1 and 0.7% of the total viticulture area (Table 2).

Implementing the 10.or.pt binary threshold revealed that approximately 25% of the overall area of viticulture regions was predicted to be climatically suitable for pest co-occurrence (Fig. 3A). Less than 7% was climatically suitable for the co-occurrence of three or more species (Table 2). The highest predicted potential for co-occurrence based on this threshold occurred between EGVM and GBM, accounting for 19% of the total viticulture area, followed by EGVM and GTM for 11% of the area (Fig. 3B, Suppl. material 1: table S4). All remaining pairs of focal species were predicted to co-occur in between 0.1 and 6% of areas. Results based on the more restrictive maxSS threshold, suggested that just 0.1% of the total viticultural area is climatically suitable for co-occurrence of multiple species, and never for more than two-species (Table 2, Suppl. material 1:

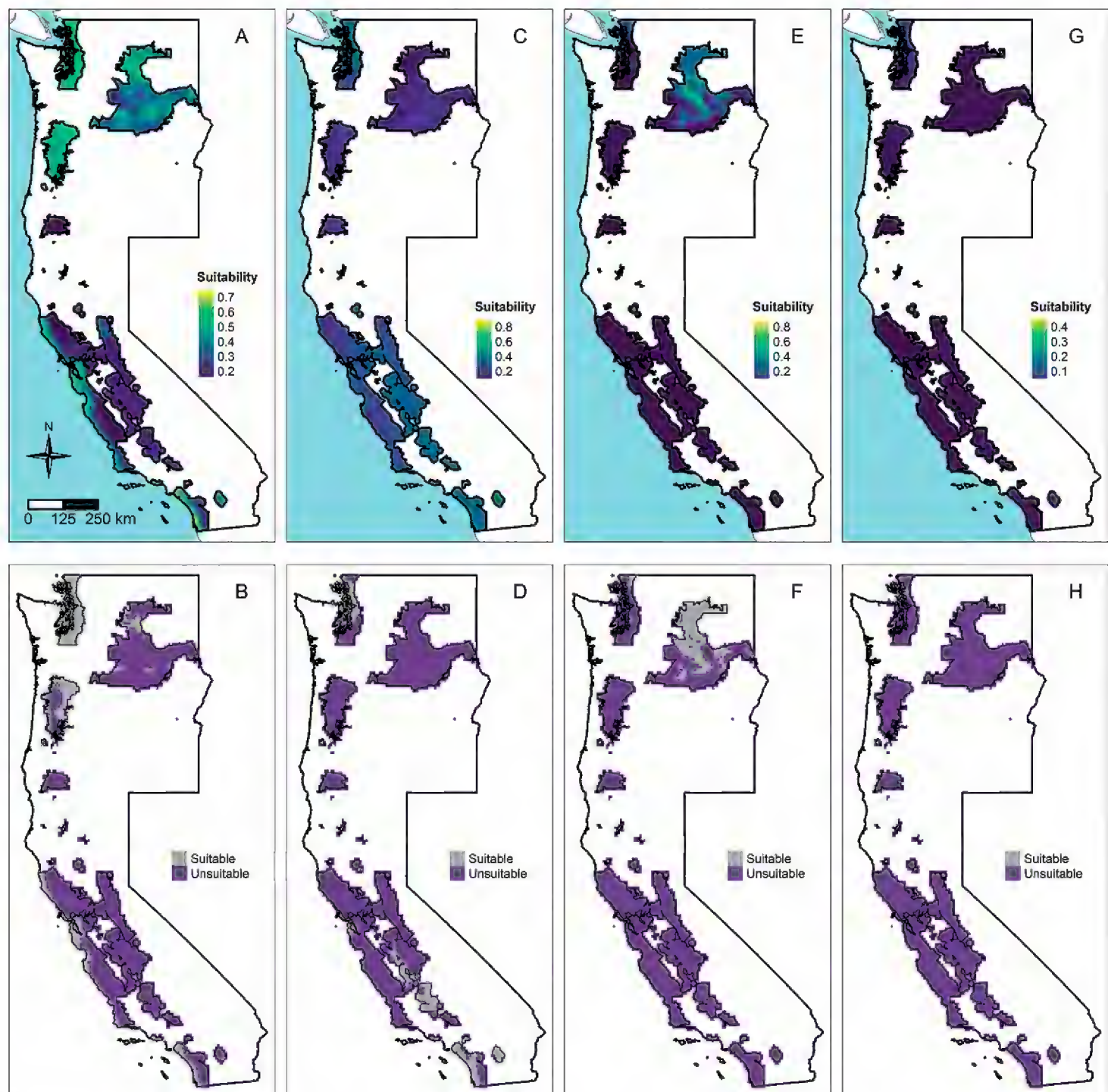


Figure 2. Climatic suitability estimates and binary predictions based on the 10-percentile lowest omission rate threshold for four moth species **A, B** grape berry moth, *Paralobesia viteana* **C, D** grape tortrix moth (GTM), *Argyrotaenia ljungiana* **E, F** European grape berry moth (EGBM), *Eupoecilia ambiguella* **G, H** Christmas berry webworm (CBW), *Cryptoblabes gnidiella*.

table S4). A PCA (Fig. 3C) was used to visualize clustering of species pseudo-occurrences relative to PCA loadings to assess qualitatively the environmental conditions underlying areas of predicted moth species co-occurrence. The results indicated: 1) an overlap in the environmental envelopes of EGBM and GBM (top left quadrant), driven mostly by annual temperature range; 2) overlapping environmental envelopes for EGVM and GTM (top right quadrant) based on mean diurnal range and minimum temperature during the warmest month; 3) an environmental envelope with less apparent multispecies overlap (i.e., more diffuse spread of pseudo-occurrences; bottom right quadrant), and 4) an environmental envelope where between three (most often EGVM, GBM, GTM) and five species may coexist (bottom left quadrant), which is driven by precipitation of the warmest quarter and to a lesser degree by precipitation during the wettest month.

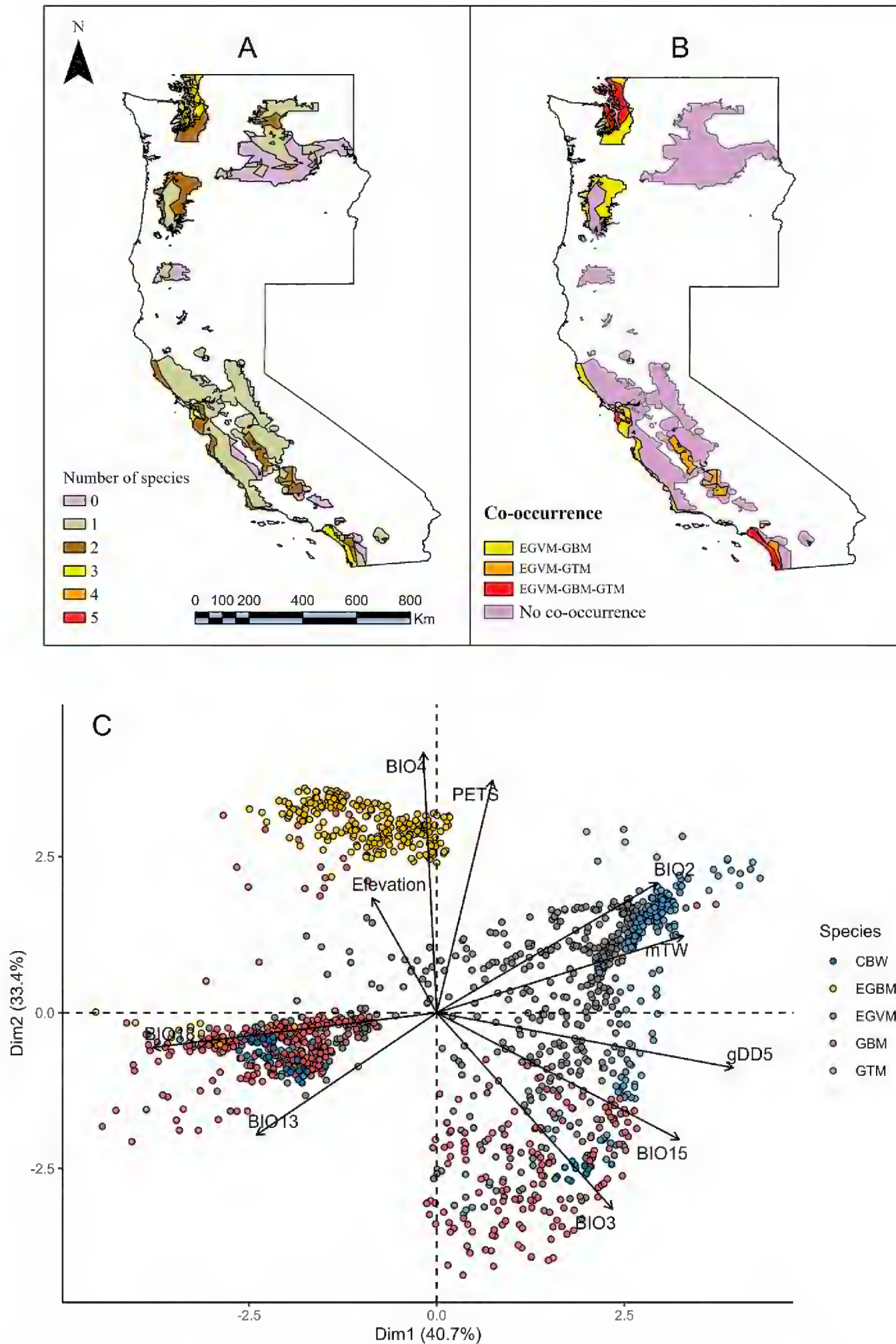


Figure 3. Regions predicted to be climatically suitable for multiple species **A** occurrence or co-occurrence of up to five of the moth species based on 10-percentile lowest omission rate thresholds **B** regions of potential co-occurrence of the three species with the highest overall suitability in the study region: European green vine moth (EGVM) *Lobesia botrana*, grape berry moth (GBM), *Paralobesia viteana*, and grape tortrix moth (GTM), *Argyrotaenia ljungiana* **C** principal component analysis depicting climatic envelopes and environmental predictors (Table 1) associated with climatically suitable areas for multispecies co-occurrence.

Discussion

Traditionally, researchers have concentrated on understanding biological invasions at large scales (Hoffmann and Courchamp 2016; Lewis et al. 2016). This approach provides fundamental knowledge of the biology of invasive species, but may offer limited predictive power at finer spatial scales (Novoa et al. 2020). Other studies have focused on the combination of pathways, invasive species traits, and characteristics of the invaded environments that underlie dynamics at finer scales, which can be used to apply specific management at regional and species levels (Kueffer et al. 2013). Identifying the environments that are most susceptible to invasion, pathways, routes, and other mechanisms that allow invasive species to establish and spread can help limit their damage (Simberloff et al. 2013; Novoa et al. 2020).

Once invasive species settle, effective management becomes difficult and costly to carry out, especially in regions affected by multiple pest species (Navia et al. 2013). Here, we focused on assessing the risk of invasion of multiple species considered to be high risk to grape-growing areas of the world, where they have caused large losses to industry (Ioriatti et al. 2012; Isaacs et al. 2012). Our analyses drew upon a comprehensive and updated collection of occurrences and utilized robust methods and strict criteria to reduce impacts of unbalanced sampling, spatial autocorrelation, and multicollinearity, to improve prediction accuracy. Our study is applicable to different invasive taxa for which the objective is to guide early detection efforts to mitigate their potential impacts (Lennox et al. 2015; N’Guyen et al. 2016).

Scientists have linked successful invasive species to high abundance, wide distribution in their native ranges, and distinct traits that ease establishment and spread (e.g., Williamson and Fitter 1996). Although all five focal species may fulfill these criteria to varying degrees, our results suggested that EGVM poses the greatest risk of establishing if reintroduced into the study region. Previous studies have shown EGVM to be highly damaging for the grape industry across its native distribution in Europe (Thiéry and Moreau 2005; Ioriatti et al. 2012; Delbac and Thiéry 2016). Our results indicate that a large portion of the study region is likely to be climatically suitable for EGVM establishment. Predicted climatically suitable areas include most viticultural areas of California, Oregon, and western Washington; particularly locations with relatively low elevations, and dry and warm seasonal conditions. Most areas of eastern Washington, where most of the grape wines are grown, were found to be climatically unsuitable for EGVM.

Our results are consistent with those of a prior global analysis of EGVM suitability (Rank et al. 2020) and a physiologically-based demographic model (Gutierrez et al. 2012, 2018), which showed high suitability for EGVM in dry and warm seasonal habitats. Our predictions also coincided in most of our study region with a new large-scale, physiologically-based demographic model developed by the Spatial Analytic Framework for Advanced Risk Information Systems (SAFARIS) for EGVM (SAFARIS 2022). Overall, the major differences in predicted climatic suitability observed between our model and the models described above can be attributed to different approaches used to generate models (correlative vs process-based), the spatial scale, as well as the selected environmental predictors. Given that management strategies

derived from predictive models are scale dependent, our model can serve as a precise framework for grape-growing regions across the West Coast of the United States. For the small set of regions that showed conflicting values of suitability among suitability maps, combined prevention strategies can be applied to prevent pest establishment. Given limited resources, higher risk areas can be prioritized for surveillance as an aid to decision making. Finally, we expect it may be important to consider horticultural practices or other management activities within specific grape-growing regions. For example, irrigation, a widespread strategy in vineyards across the Western United States, may affect suitability at very fine spatial scales, but potential effects would depend on local factors such as the frequency and quantity dependent on weather, soil type and variety. Future monitoring of environmental predictors at the site level, development of fine-scale models (e.g., remote sensing derived models), and identification of potential pathways for pest introduction and spreading would complement our analyses.

The prior invasion of EGVM in California, and its ultimate eradication, may yield important lessons for future responses to invasive insects (Schartel et al. 2019). A retrospective analysis suggested that the success of the program was attributable to a combination of efficient transfer of knowledge gained from research conducted in EGVM's native range, appropriate implementation of regulatory and control strategies, and coordinated responses among researchers, cooperative extension personnel, regulatory agencies, members of industry, and the general public (Zalom et al. 2013; Schartel et al. 2019; Simmons et al. 2021). Habitat suitability modeling using occurrence records from the most heavily invaded area, in Napa County, showed certain locations to be highly suitable for EGVM contingent on a combination of climatic conditions, attributes of the surrounding landscape, and anthropogenic variables (e.g., proximity to transportation corridors). Yet, the persistence of statistical hotspots in EGVM occurrences over time was not strongly tied to habitat suitability (Schartel et al. 2019). This pair of apparently contradictory results left open questions regarding the true suitability of the region for EGVM establishment, perhaps reflecting underlying challenges with drawing inferences in the midst of an active eradication program. Fortunately, the present study provides some clarity on this issue. Specifically, the climatic suitability predictions for EGVM indicated that not only is it well suited to those areas most heavily affected in the prior invasion, but a substantial fraction of vineyard acreage in other areas of California, Oregon, and Washington are likely at risk of EGVM establishment should it be reintroduced.

We found that in addition to EGVM, two other moth species, GBM and GTM, might find moderate expanses of climatically suitable areas. Since the expansion of grape-growing regions in North America, GBM has increased in abundance and distribution, but it has not been observed in the western United States. However, viticulture regions in Washington and Oregon seem to offer suitable conditions, as this species performs well in temperatures in seasonal humid environments (Botero-Garcés and Isaacs 2003; Isaacs et al. 2012). On the other hand, climatically suitable areas for GTM mostly occurs in Central and Southern California, specifically in dry regions with more stable temperatures across the year, which coincides with the habitats described for this species in its native and invaded range throughout the Palearctic (Ioriatti et al. 2012). Although our results showed that much of the study region is unlikely to be climatically suitable for

EGBM and CBW establishment, their inclusion in this assessment is substantiated due to their high invasiveness and similar ecology to EGVM. While EGBM has been highly successful invading mainland and islands in Asia, CBW has been reported in Asia, Africa, the Americas, and New Zealand (Ioriatti et al. 2012). Based on occurrence records, EGBM and CBW overlap and potentially interact with EGVM, at least historically, in most of their native range in Europe. Similar studies have assessed the potential distribution of invasive pathogens (Lötters et al. 2009; Turbill and Welbergen 2020), and pests (Narouei-Khandan et al. 2016) and illustrate the utility of SDMs to inform the location and timing of monitoring for potentially invasive species (Srivastava et al. 2019).

An additional benefit of this work was to model multiple species' pest risk establishment probabilities which can also aid efforts to develop tools, such as multi-lure pheromone traps, that can simultaneously monitor multiple species while reducing the costs and time-intensive nature of monitoring efforts (Epanchin-Niell et al. 2014). Ongoing research (A. Lucchi, personal communication; G. Simmons, unpublished data) is evaluating the effectiveness of pheromone traps for each moth species alone and in multi-lure combinations, given that interference between certain pheromones may influence multi-lure traps' ability to attract and detect focal species (Brockerhoff et al. 2013; Chase et al. 2018; Rowley et al. 2018). Further developments concerning the efficacy of multi-lure traps, coupled with the results of the PCA that complement the climatic suitability maps of our study species and identify variables associated with the potential suitable habitat for multispecies co-occurrence across the West Coast of the U.S., may lead to more targeted, and ultimately effective, multi-pest monitoring programs.

Although a growing number of studies have modeled the distribution of multiple species or assessed co-occurrence of multiple species through joint SDMs or occupancy models (Pollock et al. 2014; Norberg et al. 2019), the use of SDMs to assess the distribution and co-occurrence of multiple pest species remains unexplored (e.g., Briscoe Runquist et al. 2021). The accurate prediction of species co-occurrence has methodological limitations and effectiveness relies on exploratory analyses and robust methods of data collection and cleaning (Dormann et al. 2018). Previous studies have shown overlapping distributions and apparent coexistence of EGVM, EGBM, GTM, and CBW (Ioriatti et al. 2012). Similarly, the ecology and habitat characteristics of the North American GBM suggest this species might successfully invade grape-growing regions where it could potentially co-occur with other moth pests (Ioriatti et al. 2012; Isaacs et al. 2012). For invasive agricultural pests, there are always limitations on the amount of funding available to mount bio-surveillance efforts. Pest risk analysis resources and tools such as the Cooperative Agricultural Pest Survey (2022) and the climate suitability model in SAFARIS (2022), have been designed to aid decision makers to choose which pests, and in which parts of the country, to mount detection programs in order to effectively dedicate funding. While these tools are valuable to make decisions on which states may be at risk of pest establishment, the models presented here refine which grape production areas have the highest relative risk of pest establishment for several key pests to allow optimal use of scarce resources to design pest surveys. Adding information about invasion pathways would further refine efforts to optimize detection efforts in areas of the highest risk of pest arrival and establishment.

Conclusions

Detection and surveillance efforts are important components of early pest management strategies but are often costly and time-intensive (Blackburn et al. 2017). The still-substantial cost and potentially reduced efficacy of multi-lure traps means that informed decisions must be made about where to implement these efforts in at-risk regions. To this end, predictive methods such as SDM may guide pest monitoring efforts. This suggests predictive methods will still be of practical value in guiding early detection and surveillance efforts for entire pest complexes. Results of this work can be used to make preventive management more effective by identifying high and moderate risk areas for pest invasion and potential pathways of pest introduction and spread. Furthermore, this study can be used as a reference for the assessment of other pest complexes.

Our findings suggest that most resources should be used to avoid a secondary spread of EGVM in the viticulture regions of the West Coast of the United States. Additionally, given the apparent potential for coexistence of the European species in some areas (Ioriatti et al. 2012), traps embedded with multiple species' pheromones may offer a logistically easier and more cost-effective way to monitor for multiple species (Chase et al. 2018). Ongoing studies with different combinations of lures are evaluating the potential virtue of these multi-lure traps in grape moth pest monitoring programs (A. Lucchi, Personal Communication; G. Simmons, unpublished data). The results of this work can be integrated with important management tools, such as the USDA Office of Pest Management Policy (OPMP) that serve as valuable inputs into setting pest control strategies.

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Supplementary material I

Assessing the risk of invasion by a vineyard moth pest guild

Authors: Hector Zumbado-Ulate, Tyler E. Schartel, Gregory S. Simmons, Matthew P. Daugherty

Data type: figures and tables (word document)

Explanation note: **table S1.** 34 environmental variables considered during the development of species distribution models for five lepidopteran grapevine pests. **table S2.** Climatic suitability modeling methods as organized by the ODMAP framework (Zurell et al. 2020). **table S3.** Fit metrics for the most robust model of the extent of climatically suitable habitat for each of five individual moth species. **table S4.** Estimates of the extent of climatically suitable habitat in km² (and percent of total viticultural regions) shared by pairs of five moth pest species across viticulture regions of the West Coast of the United States. **figure S1.** Study region with purple polygons denoting the location of viticulture regions within the West Coast of the United States, specifically in California, Oregon, and Washington. **figure S2.** Known occurrences (orange dots) and climatic suitability estimates for the European grape berry moth, *Eupoecilia ambiguella*, across its native range in Europe. **figure S3.** Known occurrences (orange dots) and climatic suitability estimates for the European grapevine moth, *Lobesia botrana*, across its native range in Europe. **figure S4.** Known occurrences (orange dots) and climatic suitability estimates for the Grape berry moth, *Paralobesia viteana*, across its range in North America. **figure S5.** Known occurrences (orange dots) and climatic suitability estimates for the Grape tortrix moth, *Argyrotaenia ljungiana*, across its native and invaded range in Europe. **figure S6.** Known occurrences (orange dots) and climatic suitability estimates for the Christmas berry webworm, *Cryptoblabes gnidiella*, across its native range in Europe and Northern Africa. **figure S7.** Response curves of the two environmental predictors with the highest contributions to the model predictions for the European grapevine moth, *Lobesia botrana*, across its native and invaded range. **figure S8.** Response curves of the two environmental predictors with the highest contributions to the model predictions for the grape berry moth, *Paralobesia viteana*, across its native and invaded range. **figure S9.** Response curves of the two environmental predictors with the highest contributions to the model predictions for the grape tortrix moth, *Argyrotaenia ljungiana*, across its native and invaded range. **figure S10.** Response curves of the two environmental predictors with the highest contributions to the model predictions for the European grape berry moth, *Eupoecilia ambiguella*, across its native and invaded range. **figure S11.** Response curves of the two environmental predictors with the highest contributions to the model predictions for the Christmas berry webworm, *Cryptoblabes gnidiella*, across its native and invaded range.

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